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Energetic costs of social dominance in wild male baboons

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In vertebrates, glucocorticoids can be upregulated in response to both psychosocial and energetic stressors, making it difficult to identify the cause of elevated glucocorticoid concentrations when both types of stressors are present. This problem has been particularly challenging in studies of social dominance rank in wild animals. In contrast to glucocorticoids, thyroid hormone concentrations are largely unaffected by psychosocial stressors and therefore offer a better estimate of energetic challenges. Here, we measured faecal metabolites of both triiodothyronine (mT3) and glucocorticoids (fGC) in wild baboons and assessed how these hormonal profiles vary with male dominance rank. We found that alpha males have lower mT3 and higher fGC than males of other ranks, indicating sustained energetic costs of alpha status. By contrast, low-ranking males have higher mT3 but similar fGC concentrations than non-alpha high-ranking males, reflecting their lower exposure to energetic stressors but greater vulnerability to psychosocial stressors than higher-ranking males. We also found that mate-guarding of fertile females, a behaviour expressed at higher rates by alpha males, partly explains the energetic costs of high social status. These findings offer evidence of the different types of costs experienced by low- and high-ranking animals.

1. Introduction

Social dominance rank has profound effects on individual health and physiology. Initial work on captive animals revealed that low-ranking animals have elevated glucocorticoid (GC) concentrations, supporting the idea that subordinates lack predictability and control in their daily life ([1]; reviewed in [2]). However, studies in natural habitats do not consistently support this idea: the relationship between social rank and GC concentration varies across species, mating systems, and sexes [2–7]. Specifically, in the wild, high-ranking animals have higher GC concentrations than low-ranking animals in several cooperatively breeding species and in several social primate species [3,4,7–10]. Because high dominance rank is usually associated with a relatively high degree of predictability and control, another explanation is needed to account for rank-based variation in GC profiles.

Glucocorticoids are secreted in response to a wide variety of stimuli, including energetic challenges. In wild mammals, energetic stressors are at least as important as psychosocial stressors in upregulating GC secretion; this may be especially true for high-ranking animals if they perform energetically costly behaviours at high rates [7–9,11]. For example, in hierarchies where dominance is acquired and maintained through physical conflict, and mating and breeding are performed mainly by dominant animals, high-ranking individuals tend to have higher GC concentrations than low-ranking ones [2,4,5,8]. By contrast, in hierarchies in which all individuals reproduce and dominance rank is nepotistically inherited (and therefore requires less aggression to obtain and maintain), low-ranking animals tend to have higher GC concentrations [2,4,5,12].

Determination of GC concentrations alone does not allow us to differentiate between the effects of energetic and psychosocial stressors. By contrast, thyroid hormone concentrations are largely unaffected by psychosocial stressors (with the exception of some major psychiatric disorders [13]). They are regulated by energy expenditure and availability, and therefore offer a better estimate of exposure and response to energetic challenges [14–17].

Furthermore, the mode of action and regulation for triiodothyronine (T3), the bioactive form of thyroid hormones, is different from GCs. GCs mobilize energy by increasing both glucose intake (by increasing appetite) and glucose production (by mobilizing amino acids, stimulating fat breakdown and increasing gluconeogenesis). GC secretion also downregulates the storage of glucose and its use in activities that are non-essential. By contrast, T3 modulates energy usage by upregulating adenosine triphosphate (ATP) turnover and decreasing the efficiency of ATP synthesis, resulting in an elevation in basal metabolic rate and heat production. For T3 to stimulate metabolism, energy must be available through food intake or mobilization of fat stores. Consequently, when energy reserves are not depleted (e.g. when food is abundant) and the stressor is of relatively short duration, T3 concentrations increase in concert with GCs in response to an energetic challenge, leading to the mobilization of glucose that is immediately used to respond to the elevated energetic demands. However, when food is limited or energetic demands persist for long enough to nearly deplete reserves, T3 concentrations are downregulated, to avoid the exhaustion of energy reserves ([15,18,19]; see review by [13]).

Here, we measured the faecal metabolites of GCs (fGCs) and T3 (mT3) in wild male baboons to determine whether adult male baboons of different dominance ranks present distinct hormonal profiles, reflecting different energetic and psychosocial stressors. Male baboons form strong linear dominance hierarchies that are established and maintained through aggression [20,21]. Social dominance confers a fitness advantage as high-ranking males are more successful than low-ranking males at obtaining mate-guarding opportunities (i.e. ‘sexual consortships’), during which males follow, socialize, and mate with a fertile female while preventing other males from doing so [20–23]. These consortships may last from several hours to several days and impose costs on males in the form of compromised foraging opportunities [24–28]. Therefore, the fitness advantages of social dominance come with costs, including the fact that high-ranking individuals have higher fGC concentrations than low-ranking males in at least some contexts [8,29,30]. For instance, in both anubis baboons (*Papio anubis*) and chacma baboons (*Papio ursinus*), high-ranking males experienced elevated GCs specifically during periods of hierarchy instability [29,30]. By contrast, in the Amboseli baboon population (*Papio cynocephalus* with *P. anubis* admixture), alpha males had the highest fGC concentrations regardless of hierarchy stability, while high-ranking males other than the alpha tended to have consistently lower fGCs than low-ranking males [8]. In Amboseli, chronically elevated fGC concentrations are linked to reduced adult survival in female baboons [31], although the costs of elevated fGCs for males are unknown.

(a) Hypothesis and predictions

We hypothesized that the pattern we previously documented in Amboseli [8], in which alpha males had high fGC concentrations relative to other high-ranking (non-alpha) males, were the result of the sustained energetic costs of aggressive interactions and sexual consortships. These two behaviours are performed at high rates by top-ranking individuals ([20,25–28]; see the electronic supplementary material, figure S1). By contrast, we proposed that the elevated fGC concentrations in low-ranking males that we observed previously [8] reflected primarily psychosocial rather than energetic stressors.

We test four predictions of this hypothesis by comparing mT3 and fGC concentrations in adult males of all dominance ranks. First, we predicted that alpha males would have both higher fGC (as demonstrated before [8]) and lower mT3 concentrations than males of other ranks, as we expected the high energetic demands of alpha status to persist during their entire tenure and therefore T3 concentrations to be downregulated to limit the exhaustion of their energy reserves ([13,19]; see reviews [32,33]). Second, we predicted that low-ranking males would have higher fGC [8] and similar or higher mT3 concentrations than non-alpha high-ranking males, reflecting their greater vulnerability to psychosocial stressors but lower exposure to energetic stressors compared with higher-ranking males. Third, we predicted that higher rates of aggressive interactions and sexual consortships would be associated with higher fGC and lower mT3 concentrations, regardless of male dominance rank, because these behaviours result in sustained energetic costs. Fourth, we predicted that the effect of alpha status would disappear when these two behaviours were present in the model because the energetic costs of being alpha would be fully accounted for by these variables. In testing these predictions, we include as predictors a set of environmental variables known or suspected to contribute to variation in fGC and/or mT3 to learn about their relative contributions compared with dominance rank and male behaviour.

2. Methods

(a) Study population

The subjects were members of multiple social groups of a well-studied population of individually identified baboons in the Amboseli Basin in Kenya. This population consists of yellow baboons (*P. cynocephalus*) that experience natural admixture with neighbouring populations of anubis baboons (*P. anubis*); most individuals in the population have mixed genetic ancestry [34–36]. Individuals of all ancestries are included in our analyses (see the electronic supplementary material for details). We first ran all models without including measures of genetic ancestry for individuals. We next ran a subset of models with genetic ancestry as a predictor variable, but found no evidence that ancestry predicts fGC and mT3 concentrations (see the electronic supplementary material: text, tables S1 and S2).

We analysed steroid hormone and thyroid hormone concentrations in 4697 faecal samples collected between November 2004 and July 2018 from 204 adult males living in multiple distinct social groups (study groups). Approximately one-third of these samples (those collected between November 2004 and December 2008) had been previously assayed for fGC and were included in the analyses presented by Gesquiere *et al.* [8]. The present manuscript reports results that include fGC data for an additional 3224 samples, collected between 2009 and 2018. The mT3 concentrations in 4697 samples have not been previously published.

The mean number of faecal samples analysed per male ± s.d. was 23 ± 27 (range of 1–182, see also the electronic supplementary material, table S3) during a mean interval of 2.89 years per male (range = 0.08 to 11.67 years). Details on sample distribution across ages, dominance ranks and hydrological years are available in the electronic supplementary material, figure S2. Individuals in study groups are monitored on a near-daily basis, with demographic and behavioural data collected by the Amboseli Baboon Research Project (ABRP; e.g. [37], see also [38]).

(b) Hormone measurements

Faecal samples were mixed and placed in 95% ethanol immediately after being deposited by known individuals and kept refrigerated until shipment from the field site to the University of Nairobi (every two weeks). In Nairobi, samples were freeze-dried, sifted to remove vegetative matter, and stored at −20°C until transported to the US ([39,40]; full laboratory protocols are available in [41]).

To assay fGC concentrations, we extracted 0.2 g of faecal powder into 2 ml of 90% methanol and the faecal extract was purified using a prepped Oasis cartridge (Waters, Milford, MA) and stored at −20°C. The samples were then assayed for fGC by radioimmunoassay ([39,42,43]; see the electronic supplementary material and [41] for details).

To assay mT3 concentrations, we extracted 0.05 g of faecal powder into 5 ml of 70% ethanol, the supernatant was collected and the procedure was repeated once. Both supernatants were combined and thoroughly mixed. After concentrating the samples 10-fold in the T3 standard ‘0’ from the RIA kit mT3 concentrations were determined using the T3 ^{125}I kit (catalogue no. 06B254216, MP Biomedicals, Costa Mesa, CA; see the electronic supplementary material and [41] for details, and [17] for mT3 RIA validation; note that mT3 concentrations do not significantly degrade as a function of storage time in the freezer [17]). We attempted to measure T4 in baboon faeces, but concentrations of T4 metabolites (mT4) were below detection levels in our samples, even after concentrating the samples 20 times [17].

We examined the relationship between mT3 and fGC concentrations by calculating an average fGC and average mT3 concentration for each male, considering all his faecal samples, and then examining the correlation between these two values. mT3 and fGC concentrations were not statistically significantly correlated (Spearman’s $\rho = 0.074$, $p = 0.295$; electronic supplementary material, figure S3). This agreed with our expectation because the predictors of variation in these two hormones should only partially overlap.

(c) Environmental predictors: rainfall, temperature and season

The Amboseli basin (2°40′ S, 37°15′ E; 1100 m altitude) is a semi-arid short-grass savannah ecosystem located in an ancient lake basin at the base of Mount Kilimanjaro [44–47]. Daily records of rainfall were obtained using a rain gauge and daily records of minimum and maximum temperature (T_{min} and T_{max}, respectively) were obtained using a min–max thermometer, both located at the research field camp within 2–17 km of the study groups’ home ranges [48]. For each faecal sample, we calculated the total amount of rain that fell and the average daily temperature (T_{av}, the average of T_{min} and T_{max}) in the 30-day period preceding sample collection. We used T_{av} as a quadratic function in our statistical models instead of T_{min} and T_{max} because these variables were highly collinear (generalized variation inflation factors > 3; see also [47]).

Amboseli is characterized by two rainy seasons and two dry seasons each year [44–46,48,49]. In this analysis, we used a ‘four seasons’ variable in our models, instead of a ‘two seasons’ (wet/dry) variable, as our recent work showed that ‘four seasons’ explained more variance in mT3 concentrations in female baboons (see the electronic supplementary material and [47] for details). The season in which each faecal sample was collected was included in our analysis of variation in mT3 and fGC.

(d) Demographic and social predictors

(i) Male age

The birth dates of $n = 95$ (of 204) subjects that were born into study groups were accurate to within a few days or, in two cases, a few months. Because male baboons disperse from their natal group during development [50], $n = 109$ subjects were immigrants whose exact birth dates were unknown; these birth dates were estimated based on body size, coat condition, degree of scarring, body carriage and canine tooth condition. Immigrants' birth dates included an uncertainty estimate; estimates for immigrants in this study were deemed accurate to within 1 or 2 years (see [51] for details). The male's age on the date of sample collection was then determined for each faecal sample, based on either known or estimated birth dates.

(ii) Relative frequencies of aggressive interactions

As part of our regular monitoring of each study group, decided dyadic agonistic encounters between adult males were recorded continuously throughout 5 h observation sessions on each group several days per week. To measure relative frequencies of aggressive interactions across our subjects, we focused on 'aggressive/submissive' (AS) interactions in which the 'winner' of the interaction engages in overtly aggressive behaviours (e.g. physical attacks such as lunging, grabbing, biting, chasing and aggressive displays such as yawning, raising eyebrows) and the 'loser' engages only in submissive behaviours [38].

Data on these AS interactions were collected using an approach referred to as 'representative interaction sampling' in which an observer moves systematically through the group while carrying out 10 min focal animal samples according to a predefined, randomized list of focal animals, simultaneously recording all agonistic interactions in their line of sight, whether or not they involved the focal animal. This protocol is designed to avoid biases from uneven sampling of study subjects [38]. In larger groups, observer effort is more sparsely distributed across subjects (i.e. the ratio of animals to observers is larger) making it less likely that we will observe an agonistic interaction between any given pair of animals in a large group compared with a small group. Therefore, we corrected our data for observer effort, so that we were able to compare the relative frequencies of AS interactions by males across groups and across years; all of the AS interactions a male was involved in were included in calculations of relative frequency, whether the male in question won them or lost them. Specifically, we regressed the total monthly number of AS interactions for each male against observer effort, where observer effort was calculated as the number of focal samples collected in the group during that month, divided by the mean number of focal subjects in the group during that month, divided by the number of days the focal male was present in the group [31,52].

(iii) Proportion of consortship time obtained

All occurrences of sexual consortships (mate-guarding episodes) were recorded as part of our regular monitoring of each study group [38,53]. Each record includes the start and end times of the consortship. If the consortship started before and/or ended after the day's observations (i.e. its start and/or end times were censored), we assigned to the consortship the average duration time determined for all consortships of known duration. For each month and each group, we calculated the duration of all consortships that occurred within five days before the onset of the female sexual swelling deturgescence (when ovulation and conception are most likely to occur [54–56]) and considered this to represent the total consortship time of fertile females that was available to adult males. For each adult male, we totalled the duration of his consortship time for a given month and calculated the proportion of the total available consort time of fertile females that he obtained in his group.

(iv) Dominance rank

Ordinal male dominance ranks are calculated monthly for all adult males relative to other adult males in the same social group ([57]; see [58] for our detailed protocol for rank assignment). For each faecal sample, we determined the male's ordinal dominance rank for the month in which the sample was collected. In our analyses, we included dominance rank both as a continuous variable (ordinal rank) and as a categorical (alpha, i.e. ordinal rank 1, or not alpha, i.e. all other ordinal ranks). This choice was based on previous data that showed a non-linear relationship between male baboon dominance rank and fGC [8].

(v) Hierarchy stability

For comparability with Gesquiere *et al*. [8], we defined a month as 'stable' if males in each of the top three ordinal rank positions in a social group were the same as the month before and the month after. If any of the top three ordinal ranks was occupied by a different male in the month before or after, the month was defined as 'unstable'. We established hierarchy stability based on rank changes among the three highest-ranking males because, in Amboseli, 70% of conceptions on average are attributable to the three highest-ranking males [22]. For each faecal sample, we determined whether the male was in a group with a stable or unstable hierarchy in the month the faecal sample was collected.

(vi) Group size

For each faecal sample, we used the number of adult males in the group on the first day of the month the sample was collected as our measure of group size. This number ranged from 3 to 21 individuals during this study (mean ± s.d. = 10 ± 4). Only one study group had fewer than three adult males for part of the study and faecal samples from this period were excluded (16 samples).

(e) Data analysis

(i) Overview

We proposed a specific hypothesis about the effects of dominance rank on mT3 and fGC, based on our results in Gesquiere *et al*. [8], but we did not have a specific hypothesis about the relative importance of environmental variables in determining male baboon energy balance. Therefore, we used a model selection approach based on information-theoretic criteria, which offers an alternative to traditional null hypothesis testing when trying to determine the relative importance of a set of predictors that might influence a response variable [59,60]. We built four sets of linear mixed-effect models, two sets for each hormone using the 'lmer' function of the 'lme4' package of the statistical software R, version 4.0.4 [61], with hormone concentration as the response variable. Both fGC and mT3 were log transformed to approach normal distributions of the model residuals. We calculated Z-scores for our continuous predictors to have them on the same scale. We included a 'storage' variable in all our statistical models to account for variation in the period of time between faecal sample collection and the radioimmunoassay [12,17]. Mean ± s.d. storage time for mT3 was 9.02 ± 4.08 years, with a range from 0.86 to 16.74 years. Mean storage time for fGC was 0.96 ± 0.41 years, with a range from 0.24 to 2.28 years.

Our first set of models included alpha status (whether or not a male was the alpha) and ordinal dominance rank as the only behavioural predictors of hormone concentrations, with the goals of (i) recreating the results reported in Gesquiere *et al*. [8] for fGC concentrations, and (ii) determining the relative importance of dominance rank versus environmental variables for mT3 concentrations. The second set of models included two additional behavioural variables that we know are correlated with dominance rank (see the electronic supplementary material, figure S1)—relative frequency of aggressive interactions and proportion of consortship time obtained—to determine whether these behavioural variables fully account for the effect of dominance rank on fGC and mT3 in our first set of models.

(ii) Analysis 1: models with alpha status and ordinal dominance rank as the only behavioural predictors

To test predictions 1 and 2, we built one set of models for each hormone. Both sets included nine predictor variables: subject's age, ordinal dominance rank, alpha status, social group size, hierarchy stability, season, rainfall, temperature, and storage time (table 1; [8,12,17,42,43,47,62]). In each set of models, we included random effects with random intercepts for the male's identity, social group identity and hydrological year (which is defined by the beginning of the rainy season on 27 October of each year and continues through to 26 October of the following year; see table 1). We initially included two interactions among predictors (season with alpha status and season with ordinal rank), but neither interaction appeared in any of the top models; therefore, we did not include them in the final models.

We evaluated candidate models based on their adjusted Akaike information criterion ($\mathrm{AIC_c}$ values) [59]. The best model is considered to be the model with the lowest $\mathrm{AIC_c}$ value. However, all models with $\Delta\mathrm{AIC_c} < 2$ AIC units from the best model are generally considered to be equally supported [59]. These analyses were conducted using the 'dredge' function in the 'MuMIn' package in R.

After the initial information-theoretic analysis, we estimated the effect size of each parameter using full model averaging, and we assessed their relative importance by calculating the parameter-specific sum of Akaike weights, which can be interpreted as the probability that this parameter is included in the best model [60]. Finally, we estimated the variance explained by the fixed and random effects using the function 'get_variance' in the 'Insight' package in R. Collinearity among predictors was assessed by calculating the GVIF with the 'car' package in R. The GVIFs for all Z-scored predictor variables were less than 3.

(iii) Analysis 2: models with aggression and consortship as additional behavioural predictors

Next, to test predictions 3 and 4, we constructed two additional sets of linear mixed-effect models, one for each hormone. Each set included the same nine predictor variables as in analysis 1, as well as two additional behavioural variables: relative frequency of aggressive interactions (corrected for observer effort) and proportion of consortship time obtained. As in analysis 1, candidate models were evaluated based on their $\mathrm{AIC_c}$, and the effect of each parameter was estimated using full model averaging as well as by calculating their relative importance (sum of weights) across candidate models with $\Delta\mathrm{AIC_c} < 2$. The GVIFs for all predictor variables were less than 3.

(f) Compliance with animal welfare guidelines and Kenyan legislation

All data collection procedures were non-invasive, adhered to the laws and guidelines of Kenya (research permit NACOSTI/P/22/22332), and were approved by the Animal Care and Use Committee at Duke University (IACUC A028-12-02).

Table 1. Potential predictors of hormone concentrations; see §2 for detailed descriptions. (Detailed results for each predictor variable are provided in the electronic supplementary material, tables S5 and S7.)

	predictor	predictor description	predicts hormone concentrations?
environmental variables	season	four seasons defined as follows (see the electronic supplementary material): 'short rain'; 27 Oct–31 Jan, 'short dry': 1 Feb–28-29 Feb, 'long rain': 1 Mar–15 May, 'long dry': 16 May–26 Oct	**mT3—yes** fGC—no
	rainfall	cumulative rainfall in the 30 days prior to sample collection	**mT3—yes** fGC—no
	temperature	average daily temperature (T_{av}) in the 30 days prior to sample collection	**mT3—yes** fGC—no
method	sample storage	number of months the sample was stored before assay	mT3—no fGC—no
group characteristics	group size	number of adult males in the group in the month the sample was collected	**mT3—yes** fGC—no
	hierarchy stability (HS)	hierarchy was 'stable' or 'unstable' in the month the sample was collected	mT3—no fGC—no
male traits	age	age of the male at the time the sample was collected	mT3—no fGC—no
behavioural variables	alpha status ordinal rank	whether the male occupied the top ranking (alpha) position or not in the month the sample was collected ordinal dominance rank of the male in the month the sample was collected	**mT3—yes for both alpha and ordinal rank**, after controlling for the proportion of consortships obtained **fGC—yes for alpha but not for ordinal rank**; the alpha effect is accounted for by proportion of consortships obtained
	consortships	proportion of consortship time a male obtained in the month the sample was collected	**mT3—yes**, but in opposite direction to predicted **fGC—yes**
	aggression (AS)	the male's relative frequency of aggression, controlling for observer effort	mT3—no fGC—no
random effects	hydrological year	hydrological year in which the sample was collected (begins on 27 Oct of each year; e.g. hydrological year 2005 begins on 27 Oct 2004 and continues through to 26 Oct 2005)	
	male ID	identity of the male from which the faecal sample was collected	
	group ID	identity of the group the male was in when the faecal sample was collected.	

3. Results

(a) Analysis 1: models with alpha status and ordinal dominance rank as the only behavioural predictors

(i) Sources of variance in mT3 concentrations

Ten of our candidate models for mT3 (hereafter the 10 'top models') produced ΔAIC_c values within two units of the model with the lowest AIC_c (figures 1*a* and 2*a*; electronic supplementary material, tables S4, S5 and figures S4a, S5). Both ordinal rank and alpha status appeared in eight of these 10 top models, although their full model-averaged estimates showed confidence intervals (CIs) that overlapped zero (estimate = 1.6%, 95% CI = −0.5 to 3.7% for ordinal rank and estimate = −3.0, 95% CI = −7.5 to 1.6% for alpha status). In other words, ordinal rank and alpha status may predict mT3 concentrations, but their effects carry high uncertainty.

Social group size appeared in all top models, indicating a high confidence that group size predicted mT3. For each increase of 1 s.d. in group size, mT3 concentrations decreased on average by 3.1% (95% CI = −5.1 to −1.1%). By contrast, hierarchy stability only appeared in half of the top models and its model-averaged estimate showed confidence intervals that overlapped zero (estimate = 0.8%, 95% CI = −1.4 to 3.9%), providing little support that hierarchy stability predicted mT3 concentrations.

Rainfall, temperature and season were robust predictors of mT3 concentrations: they appeared in all top models. For each increase of 1 s.d. in rainfall, mT3 concentrations increased by 5.6% (95% CI = 4.2 to 7.1%). The effect of temperature was best described by a quadratic term, with lower mT3 concentrations in the coolest and hottest months. Season also explained variance in mT3, even after accounting for the effects of rainfall and temperature in our model: mT3 concentrations were on average 4.3% lower during the long dry season than during the short rainy season (95% CI = −8.2 to −0.5%), and 5.9% lower during the short dry season than during the long dry season (95% CI = −10.4 to −1.1%). Neither time in storage nor male age emerged as

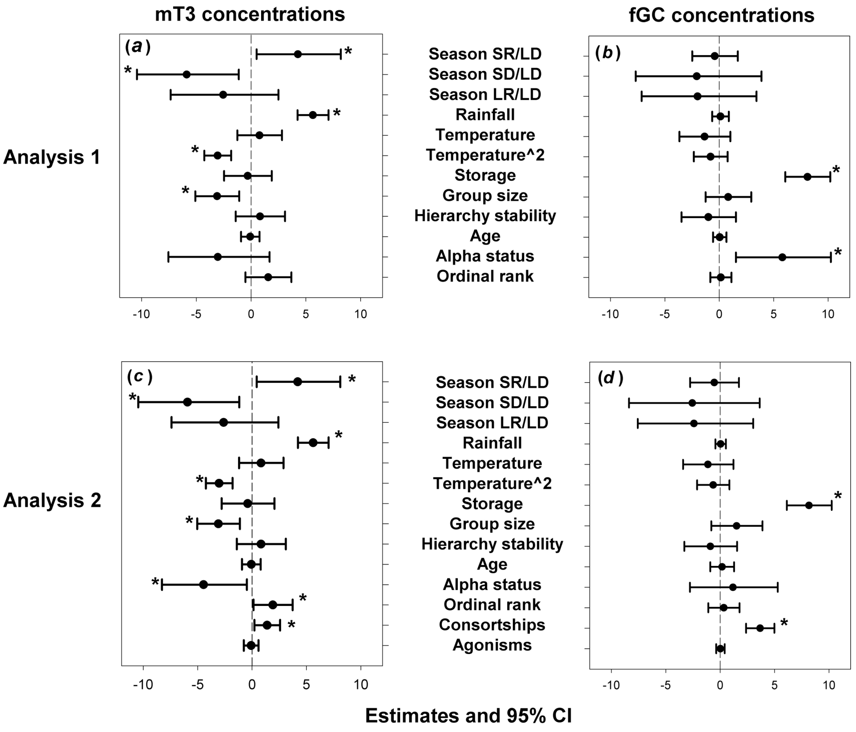

Figure 1. Model averaged estimates and 95% confidence intervals (CIs) for predictors of mT3 and fGC concentrations. Analysis 1: models with alpha status and ordinal dominance rank as the only behavioural predictors: (*a*) mT3 results; (*b*) fGC results; analysis 2: models with aggression and consortship as behavioural predictors: (*c*) mT3 results; (*d*) fGC results. An asterisk indicates predictors for which 95% CI do not overlap zero.

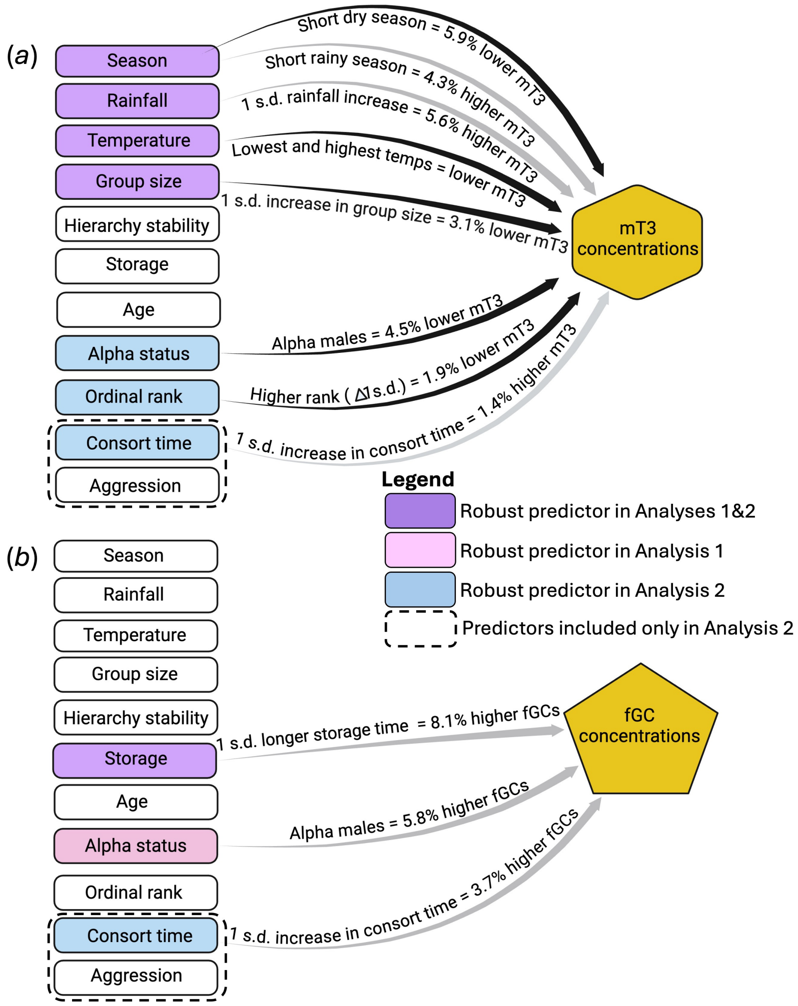

Figure 2. Environmental and behavioural predictors of (*a*) mT3 concentrations and (*b*) fGC concentrations. Grey arrows show positive relationships, black arrows show negative relationships. 'Robust' predictors are those whose 95% CIs do not overlap zero. Predictors within dashed boxes were included only in analysis 2; all other predictors were included in both analyses. See figure 1 and the electronic supplementary material, tables S5 and S7 for detailed results. Created with BioRender.com.

important predictors of mT3 concentrations; they appeared in two of the top models and had small model-averaged estimates with confidence intervals that overlapped zero.

(ii) Sources of variance in fGC concentrations

Twenty-three of our candidate models explaining variation in fGC produced ΔAIC_c values within two units of the model with the lowest AIC_c (figures 1*b* and 2*b*; electronic supplementary material, tables S4 and S5, figures S4b and S5). Alpha status was a robust predictor of fGC concentrations appearing in all 23 top models. In support of our first prediction, fGC concentrations were on average 5.8% higher for alpha males than males of other ranks (95% CI = 1.5–10.3%) [8]. By contrast, ordinal rank was only in six top models, and contrary to our second prediction that low-ranking males would have higher fGC than high-ranking males, we found no marked effect of dominance rank on fGC concentrations beyond the alpha effect [8].

Group size and hierarchy stability appeared in just over half of the top models. However, their model-averaged estimates showed CIs that overlapped zero (estimate = 0.8%, 95% CI = −1.2 to 2.9% for group size and estimate = −1, 95% CI = −3.5 to 1.5% for hierarchy stability). In contrast to previous studies, we saw little indication that season, rainfall and temperature predicted fGC concentrations. Season and rainfall appeared in less than 40% of the top models and the confidence intervals of their model-averaged estimates overlapped zero. While temperature appeared in over 60% of the top models, the confidence intervals for its model-averaged estimates overlapped zero.

Age was present in only three of the top models and its model-averaged estimate was close to zero, providing little support that age-predicted fGC concentrations. As in a previous study [12], we found that time in storage strongly predicted fGC concentrations, appearing in all the top models. fGC concentrations increase an average of 8.1% for each 1 s.d. increase in storage time (95% CI = 6.1–10.2%).

(b) Analysis 2: models with aggression and consortship time as additional behavioural predictors

(i) Sources of variance in mT3 concentrations

In analysis 2, eight ‘top models’ for mT3 concentrations produced a $\Delta AIC_c < 2$ (figures 1*c* and 2*a*; electronic supplementary material, tables S6 and S7). Contrary to prediction 3, we found no evidence that males with relatively high frequencies of aggressive interactions had lower mT3 concentrations; aggression appeared in only two of eight top models. By contrast, the proportion of consortship time obtained was high in all top models. However, its effect was in the opposite direction to our prediction: mT3 concentrations were on average 1.4% higher for each 1 s.d. increase in consortship time (95% CI = 0.2–2.6%).

Contrary to prediction 4, when consortships and aggression were included in the model, both alpha status and ordinal rank appeared in all top models, and the CIs of their model-averaged estimates did not overlap with zero. mT3 concentrations were on average 4.5% lower for alpha males than for males of other ranks (95% CI = −8.3 to −0.5%). Furthermore, mT3 concentrations were also lower for other high-ranking males (not just the alpha) than for low-ranking males. Specifically, mT3 concentrations were 1.9% higher (95% CI = 0.3–8.0%) for each increase of 1 s.d. in ordinal rank, where an increase in ordinal rank value equates to a drop in social status (e.g. a change from rank 1 to rank 2 is an increase in ordinal rank value). Results for all other variables, including group size, season, rainfall and temperature, were similar to analysis 1.

(ii) Sources of variance in fGC concentrations

Forty-two models produced a $\Delta AIC_c<2$ (figures 1*d* and 2*b*; electronic supplementary material, tables S6 and S7). The proportion of consortship time obtained was a robust predictor of fGC concentrations, appearing in all 42 top models. In support of our third prediction, fGC concentrations were 3.7% higher for each 1 s.d. increase in consortship time (95% CI = 6.1–10.3%). As with mT3 concentrations, we found little evidence that the relative frequencies of aggressive interactions predicted fGC concentrations (present in only four of the top 42 models, estimate = 0.02%, 95% CI = −0.4 to 0.4%).

In support of our fourth prediction, alpha status no longer appeared to predict fGC concentrations when the proportion of consortship time obtained was included in the model. Specifically, alpha status appeared in fewer than 40% of top models and the CIs for its model-averaged estimate overlapped zero (estimate = 1.2%, 95% CI = −2.8 to 5.3%). For all other variables, results were similar to those reported in analysis 1, with no support that any of these variables predicted fGC concentrations.

4. Discussion

(a) Alpha males experienced both persistent and acute energetic challenges

In support of our first prediction, alpha males had higher fGC concentrations and lower mT3 concentrations than other males, especially after accounting for the proportion of consortship time they obtained. These results indicate that alpha males experience consistent exposure to energetic challenges to a greater extent than other males. Alpha males invest heavily in reproduction, and they also invest heavily in immune function: they heal faster [63] and express genes involved in inflammation and innate immunity at higher rates than lower-ranking males ([64,65]; see also [66]). These rank-specific patterns of energetic investment involve benefits and costs: persistent exposure to energetic challenges will eventually have negative effects on individuals. In support, previous studies in the Amboseli baboon population have found that high-ranking males have higher rates of epigenetic ageing [67] and shorter lifespans than lower-ranking males [31].

We found only partial support for prediction 4, that the energetic costs of being an alpha male would be fully accounted for by their investment in aggression and consortships. When we included these in the model, the 'alpha' effect disappeared for fGC but increased for mT3. That is, alpha males were indistinguishable from other males in their fGC concentrations in this model, implying that their greater investment in these behaviours fully accounted for their distinct fGC profiles. However, alpha males had mT3 concentrations 4.5% lower than other males in this model, compared with only 3.0% lower in models that did not include these behavioural variables. This result suggests that while more time spent in consortships is generally associated with an enhanced energetic profile, this is less true of alpha males than males of other ranks.

(b) Cost and benefits of social subordination

In partial support of prediction 2, we found that low-ranking males had higher mT3, suggesting they were less energetically challenged than higher-ranking males. Furthermore, while we failed to replicate our previous finding that low-ranking males had higher fGC than high-ranking (non-alpha) males [8], we found that low-ranking males had *similar* (rather than lower) fGC concentrations. The combination of higher mT3 and similar (although not higher) fGC, still supports our hypothesis that in subordinates, GC may be secreted primarily in response to psychosocial stressors [1,2]. The differences between this and our previous study [8] with respect to fGC concentrations may result from differences in the dataset as well as from natural variation in environmental conditions, group size and home range [47,49,68], as the two studies encompass different time periods (years 2000–2008 for [8] and 2005–2018 in this study).

(c) The energetic costs of consortships in male baboons

Our results for prediction 3 were surprising. We predicted that males with higher frequencies of aggressive interactions and more time in consortships would have a combination of low mT3 and high fGC, reflecting persistent energetic demands of these behaviours. In contrast to our prediction, however, we found no evidence that aggressive interactions predicted mT3 or fGC concentrations. Time in consortships, on the other hand, explained variation in both mT3 and fGC concentrations, but the results for mT3 were in the direction opposite to our prediction: males that obtained a higher proportion of consortships had higher, rather than lower, mT3 concentrations than other males. At the same time, our prediction for fGC was fully supported: males that obtained a higher proportion of consortship time had higher fGC than males that had less consortship time.

These results help shed light on the long-standing question about how costly consortships are for male primates. Several studies have suggested that consortships are energetically costly as they affect males' feeding time, energy balance, and GC concentrations [28,30,69–71]. However, when directly measuring energy status using C-peptide determination, Girard-Buttoz *et al*. [72] found no evidence that mate-guarding predicted C-peptide concentrations in long-tailed macaques (*Macaca fascicularis*) despite evidence that mate-guarding reduced fruit consumption and feeding time [72]. In fact, to compensate for the decrease in energy intake during consortships, male macaques appeared to reduce their energy expenditure by decreasing vertical locomotion [72].

Our results—that obtaining a higher proportion of available consortship time in the group was associated with higher fGC and *higher* (rather than lower) mT3 concentrations—support a scenario in which only males with relatively good energy reserves (i.e. who are able to upregulate TH) engage in consortships. They also suggest that consortship was associated with relatively acute (rather than sustained) energetic costs ([13]; see also reviews [32,33]).

Our original prediction—that high consortship activity would be associated with low mT3 concentrations, reflecting sustained energy expenditure—arose from the observations that (i) baboons are non-seasonal breeders and female baboons cycle asynchronously throughout the year; often resulting in extended periods of time in which mating opportunities are present, and (ii) one or a few males in a social group often account for the large majority of consortship activity [20,23]. However, although alpha and high-ranking males obtain a large proportion of consortships, they typically consort less than predicted by a strict priority-of-access model, in which male dominance ranks represent a queue for mating opportunities [20,56,69,72]. Our result for mT3 suggests that this failure of alpha and other high-ranking males to mate guard as much as predicted may be partly explained by the fact that only males with the largest energy reserves are able to engage in mate-guarding.

(d) Why are aggressive interactions not energetically costly in male baboons?

Aggressive behaviours have traditionally been considered energetically costly. Not surprisingly, in species for which dominance rank is obtained and maintained through high rates of aggression, studies have reported elevated GC concentrations in more aggressive individuals—usually the dominant animals (e.g. in most social carnivores [7]; in chimpanzees, *Pan troglodytes* [9,10]; and in a number of cooperatively breeding primates reviewed in [3]).

However, aggressive interactions can vary in their duration and frequency as well as in their intensity. For example, in chimpanzees, the charging display, the most frequent form of male aggression, used in both acquiring and maintaining dominance rank involves extended periods of running, dragging or throwing branches, swaying vegetation, and stomping or slapping the ground, behaviours that are probably energetically costly [10]. By contrast, baboons use energetically costly aggressive behaviours (e.g. lunging, grabbing, biting, chasing) only briefly to establish and maintain dominance rank, and rely thereafter to a great extent on less costly behaviours such as yawning, raising eyebrows (baboons: *P. cynocephalus*/*P. anubis* admixture [6,21,73]). Our results suggest that aggressive behaviours do not impose a substantial energetic cost on male baboons, perhaps because males mitigate the energetic costs of aggression by using aggressive displays that are not energy intensive instead of energetically costly aggressive behaviours.

(e) Other predictors of mT3 concentrations

While the focus of our analysis was social behavioural influences on mT3 concentrations, we also included group characteristics and environmental predictors of mT3 concentrations in our models. Our results for these other predictors were in agreement with previous results in our population and others: mT3 concentrations were low during periods of low rainfall, during both the hottest and coolest periods of the year, and when males lived in larger groups (table 1, figures 1 and 2; see the electronic supplementary material, tables S5 and S7, figure S5, for discussion).

In contrast to these environmental effects, we found no evidence that hierarchy instability affected hormone concentrations, even though periods of hierarchy instability may be both a psychosocial and an energetic stressor for male baboons. This result could be related to our relatively narrow definition of hierarchy instability (which follows [8] for comparability), which does not take into account rank challenges that do not produce rank reversals. This remains an area for future research.

5. Conclusions

Our study reveals that alpha males experience persistent energetic costs that are at least in part associated with mating effort. While being high ranking has benefits for males in terms of mating and paternity success, our analysis demonstrates that it also imposes costs. The energetic costs may contribute directly to the shorter lifespans and faster epigenetic ageing that we have previously reported in Amboseli male baboons [31,67]. Low-ranking males, while being less energetically challenged than high-ranking (non-alpha) males, are probably exposed to more psychosocial stressors.

Ethics. All data collection procedures were non-invasive, adhered to the laws and guidelines of Kenya, and to the Guidelines for the Treatment of Animals in Behavioural Research and Teaching established by the Animal Behaviour Society (2012). Our research is approved by the Institutional Animal Care and Use Committees (IACUC A028-12-02) at Duke University and the University of Notre Dame. This work is conducted under permits to Susan Alberts from the Kenya Wildlife Training and Research Institute (WRTI), Kenya Wildlife Service (KWS), Kenya National Environment Management Authority and Kenya National Commission for Science, Technology and Innovation (Research Permit NACOSTI/P/22/22332).

Data accessibility. The data are available at the Duke Data Repository [74].

Supplementary material is available online [75].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. L.R.G.: conceptualization, data curation, formal analysis, methodology, validation, visualization, writing—original draft, writing—review and editing; C.A.: data curation, investigation, resources; G.Y.: investigation, resources; C.B.: investigation, resources; S.P.: investigation, resources; E.E.J.: investigation, resources; T.L.W.: investigation, resources; V.K.O.: investigation, resources; R.S.M.: investigation, resources; J.K.W.: investigation, resources; I.L.S.: investigation, resources; A.C.M.: funding acquisition, writing—review and editing; E.A.A.: funding acquisition, writing—review and editing; S.C.A.: conceptualization, funding acquisition, supervision, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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